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Strawberry malformation and the tarnished plant bug

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STRAWBERRY MALFORMATION AND THE TARNISHED PLANT BUG

by

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DISSERTATION

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PREFACE

This work was published in four separate, peer-reviewed, refereed articles. They comprise chapters two through four of this dissertation and appear in the same format in which they were published. For that reason, each chapter has a brief literature review associated with it, in addition to the more detailed review of the literature that comprises chapter one.

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ABSTRACT

STRAWBERRY MALFORMATION AND THE TARNISHED PLANT BUG

by

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University of New Hampshire, May 1993

Experiments were designed to study the malformation of strawberries, *Fragaria x ananassa* (Duchesne) caused by the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois). In greenhouse experiments, duration of blossom exposure to tarnished plant bug affected the type of malformation observed. Exposure at anthesis for 48 hours was most likely to cause apical seediness, the malformation associated with tarnished plant bug. The number of nonviable achenes per fruit increased with longer feeding durations. Malformation was also affected by blossom stage. Prebloom feeding caused blossom death. Feeding at petal fall or achene separation resulted in malformations, including apical seediness. Feeding at later stages caused little damage.

Light and scanning electron microscopy were used to assess tarnished plant bug feeding on strawberries. During early fruit development stages, insects fed upon achenes. On further developed fruit, feeding sites changed to receptacle tissue. Achene injury during early fruit stages is the most likely cause of apical seediness. Feeding

during later stages caused localized cellular damage, resulting in indentations on the receptacle.

Twenty strawberry cultivars grown in a matted row trial were evaluated for susceptibility to tarnished plant bug injury. A wide range of injury was observed. 'Honeoye', 'Sparkle', 'Veestar' and 'Canoga' had significantly less injury than other cultivars. 'Mic Mac', 'Scott', 'Blomidon' and 'Redchief' were most susceptible. Cultivars with the least injury tended to have the greatest marketable yields.

Six strawberry cultivars, observed to vary in damage from tarnished plant bug injury were grown under three insecticide regimes (three sprays, one spray and no spray) to determine how differences in vulnerability might affect conventional chemical controls. Cultivars most susceptible to damage harbored more nymphs than less susceptible cultivars. Differences among cultivars were greatest when no insecticide was applied. 'Honeoye' and 'Sparkle' had the least apical seediness, followed by 'Redchief', 'Guardian' and 'Kent'. 'Mic Mac' consistently had the highest level of injury. Reducing insecticide applications did not increase apical seediness for cultivars exhibiting low susceptibility.

INTRODUCTION

The commercially cultivated strawberry, *Fragaria x ananassa* Duchesne, produces an aggregate fruit comprised of numerous achenes which rest upon an enlarged receptacle. Fruit development can be seriously disrupted by the tarnished plant bug, *Lygus lineolaris* Palisot de Beauvois, which feeds on the flowers. Affected fruit are characteristically malformed, with a concentration of achenes at the apical end. Such fruit, often called "buttons", are unmarketable and may approach 100% of a crop if high populations of tarnished plant bug go unchecked.

Little is presently known regarding the nature of tarnished plant bug feeding on strawberries, and whether susceptibility to the injury varies among cultivars. Such information is prerequisite to the development of management strategies that would offer alternatives to conventional insecticide applications.

Greenhouse, laboratory and field experiments were designed to examine tarnished plant bug feeding on strawberry and the resulting damage, to determine if cultivars differ in susceptibility to the characteristic injury, and to determine if any such differences could be used to modify insecticidal control of this insect.

While the studies presented here measured the relative susceptibility to tarnished plant bug injury among different strawberry cultivars, the mechanisms controlling such differences were not pursued in detail. Therefore, the term "resistance" is used in these articles only to express the differences observed among cultivars within the conditions of the experiments.

CHAPTER I

REVIEW OF THE LITERATURE

Strawberry Flower and Fruit Development

The strawberry inflorescence is a modified stem or cyme, terminated by a primary blossom. Branches arise at nodes from buds in the axils of modified leaves or bracts. Each branch is terminated by a blossom. Following the primary blossom, there are typically two secondaries, four tertiaries and eight quaternaries. The exact scheme may vary among cultivars or locations (Avigdori-Avidov, 1986; Darrow, 1966). An individual blossom typically has ten green sepals, five white petals and 20 to 35 stamens arranged in a spiral pattern in three whorls. The pistils are arranged spirally on the receptacle, with numbers ranging from 60 to 600. The greatest number of pistils occurs on the primary blossom and decreases successively down the inflorescence (Avigdori-Avidov, 1986; Darrow, 1966; McGregor, 1976). Each carpel bears a style inserted laterally, which extends well above the ovary. Both staminate and pistillate forms of *Fragaria x ananassa* exist, usually the result of degeneration at some point in development, but are not presently of commercial importance (McGregor, 1976; Valleau, 1918).

Strawberries are self-fertile. Pollen is mature prior to the opening of the anthers, but is not released for several days, encouraging cross pollination. Stigmas remain receptive to pollen for eight to ten days (Avigdori-Avidov, 1986; Valleau, 1918). Despite self-fertility, strawberry size and yield have been shown to increase when cross pollinated by insects (Connor and Martin, 1973). Fertilization occurs 24 to 48 hours after pollination (Darrow, 1966).

Each carpel contains one ovary, which bears one ovule and therefore, following fertilization, will contain a single embryo. This structure is an achene. Achenes are the true fruits of the strawberry. Together with the receptacle they form an aggregate, popularly termed a berry. Achenes are attached to the receptacle by fibro-vascular strands and the epidermis. They consist of a hard, five-layered pericarp, a thin, two layered testa, and a single-layered endosperm. The bulk of the embryo is in two large, semi-elliptical cotyledons, which contain large amounts of protein and fat, but no starch (Winton, 1902).

Following fertilization, the receptacle swells to form the edible part of the "berry." The receptacle is made up of an epidermal layer, a cortex and a pith. The latter two layers are separated by vascular bundles that run throughout the cortex to supply nutrients to the developing embryos. The epidermis varies in thickness depending on cultivar, and consists of polygonal, isodiametric cells. Hairs can usually be found on this layer, but stomata are rare. The cortex forms the bulk of the ripe fruit. Cell division occurs at the hypoderm on the outer edge of the cortex. The vascular bundles consist of elongated, thin-walled cells, and spiral and annular vessels. The pith is characterized by large cavities formed by the pulling apart of cells during rapid growth (Winton, 1902).

Cells in the cortex and pith are isodiametric and responsible for most of the receptacle growth. Cell size increases toward the inner part of the fruit. The cortex develops more rapidly than the pith, and 100 percent faster than the fruit as a whole. Cell division accounts for only 15 to 20 percent of the total growth, occurring mostly prior to anthesis. Approximately ninety percent of the subsequent growth is a result of cell enlargement (Havis, 1941). Sugars, aromatic compounds and pigments all increase as the receptacle tissue matures. Ripening, from anthesis to harvest stage, lasts approximately 30 days, depending on environmental conditions (Darrow, 1966).

Development of the receptacle is controlled by growth regulators, primarily auxin, which are synthesized in the achenes. Auxin is produced in the endosperm and translocated into the receptacle tissues, stimulating growth via cell enlargement (Archbold and Dennis, 1985; Lis et al., 1978; Nitsch, 1950; Southwick and Poovaiah, 1987). Removal of achenes after fertilization results in a proportionate reduction in growth. For example, leaving only three achenes on a receptacle results in three areas of growth, directly below and surrounding those achenes. A ring of achenes left on a receptacle results in a ring of growth, and so forth (Nitsch, 1950).

The ultimate size and shape of a strawberry is thus a function of the number of achenes on the receptacle, the area of receptacle tissue surrounding each achene, and the distribution of the achenes on the receptacle. Receptacles with few achenes will be small, as is observed for those lowest on the inflorescence. Berries which initiate more receptacle growth per achene will be larger. Location of the achenes on the receptacle will affect the distribution of growth, and therefore berry shape (Webb et al., 1978).

Lack of fertilization or damage to the achenes on a strawberry blossom will prevent the synthesis of auxin and result in uneven development or malformation of the receptacle. The degree and character of the deformity will depend on the number and location of damaged achenes (Parker et al., 1978). Fertilization may be blocked by reduced pollen production, nonviability of pollen, lack of pollen transfer to the stigmas, or nonreceptivity of the pistils (Brack, 1968; Darrow, 1966; Gilbert and Breen, 1986; Valleau, 1918). Such occurrences may be genetic in nature or the result of environmental conditions. Fertilization may also be affected by pesticide applications. Certain fungicides have been shown to reduce pollen viability and increase strawberry malformation (Khanizadeh and Buszard, 1987). Insecticides can reduce the number of pollinating insects, increasing the amount of deformed berries (Connor and Martin, 1973; Moore, 1969). Injury to the developing receptacle tissue can also cause berry malformation. Strawberry flowers fed on by cutworms developed holes or grooves as the berries matured due to injury to the receptacles (Howitt et al., 1965).

The Tarnished Plant Bug, *Lygus lineolaris* Palisot de Beauvois

The tarnished plant bug belongs to the family Miridae in the order Heteroptera, known as "true bugs." The assignment of genus and species has changed numerous times, but *Lygus lineolaris* has been widely accepted since 1952 (Stewart and Khoury, 1976). This insect undergoes three major life stages: egg, nymph and adult. The eggs are approximately one mm long and flask-shaped. They are typically inserted in plant stems just below the surface, or with the anterior end slightly protruding. Nymphs emerge from the eggs 10 to 14 days after oviposition. The nymphs pass through five instars before becoming adults. The first instar is approximately one mm in length and may vary in color from yellow to dark green. As each instar proceeds, size increases and wing pads develop. Adults are approximately 5 mm long and 3 mm wide. Color can vary greatly, ranging from light bronze to nearly black, with more or less distinct lines along the head and thorax. Only adults can fly and reproduce (Brittain and Saunders, 1917; Crosby and Leonard, 1914; Kelton, 1975).

According to Kelton (1975), the distribution of tarnished plant bug includes all of the agricultural regions of North America. Based on records of tarnished plant bug host plants by states and provinces, Young (1986) found this statement to be true and suggested that areas not reporting tarnished plant bug hosts lacked research on the subject.

In the northern United States and Canada tarnished plant bugs overwinter as adults under refuse or among the leaves of low-growing perennial plants. The insects become active in the early spring, from late March to early April, feeding on emerging plant buds and mating. Oviposition typically begins in early May. Each female lays between five to fifteen eggs, distributing them among the stem tissue of leaves and flowers. Nymphs appear from mid- to late May, but may not reach high numbers until late June. A second generation of nymphs follows, which peaks about late July. A third generation may appear about the middle of September, but it is doubtful that many survive. The average generation time varies from 20 to 30 days with considerable overlap. The overwintering population is probably made up of second generation adults and perhaps some third generation adults. Survival rate of the overwintering population is thought to be quite low (Brittain and Saunders, 1917; Crosby and Leonard, 1914; Ridgeway and Gyrisco, 1960; Stewart and Khoury, 1976).

The tarnished plant bug has an extremely wide range of hosts. Taksdal (1961) cited 123 plant species known to serve as hosts, but Young (1986) listed 385 plant hosts, including at least 130 economically important species, and 21 out of 30 of the most important crops in the United States. Young suggested that tarnished plant bug has the broadest documented feeding niche of any arthropod. How tarnished plant bugs recognize a suitable host is not fully understood. Prokopy and Owens (1978) observed that attraction to a host is not visual, i.e., based on color or shape. Once on a host plant, suitability is determined through chemoreceptors on the sensilli of the insects' rostrum (Ave et al., 1978).

The preferred feeding sites for tarnished plant bug on a host plant are the meristematic tissues and developing flowers and fruit (Crosby and Leonard, 1914; Tingey and Pillemer, 1977; Young, 1986). The type of injury caused by phytophagous *Lygus* species as characterized by Tingey and Pillemer (1977) includes localized wilting and necrosis, abscission of fruiting forms, morphological deformation of fruit and seed, altered vegetative growth, and tissue malformations. These species feed by a "lacerate and flush" method (Miles, 1972). Fine stylets are inserted into the plant tissue and penetrate both inter- and intracellularly. Repeated plunging of the stylets during feeding may render considerable physical damage to the tissue (Flemion et al., 1954). In addition, enzymes such as pectinase may be injected into the tissue via saliva, causing further cellular breakdown (Miles, 1972; Smith, 1920; Strong, 1970; Varis, 1972). Opinions vary regarding which of these two mechanisms is most responsible for the final degree of injury, some favoring the mechanical aspects (Flemion et al., 1954; Varis, 1972) others citing enzymatic action (Smith, 1920; Strong, 1970). Varis (1972) observed that piercing sugar beet tissue with a fine needle and applying pectinase resulted in symptoms more like *Lygus* feeding than piercing alone. It is questionable however, whether the amount of damage done by a single piercing was comparable to the extensive stylet thrusting observed by Flemion et al. (1954).

Some research has also suggested that interference with the synthesis or actions of plant growth regulators may be a primary cause of plant injury by *Lygus* species (Miles, 1972). Pod abscission on bean plants caused by tarnished plant bug feeding could be prevented by applications of naphthalene acetic acid (Fisher et al., 1946). Allen (1947) suggested that *Lygus* feeding on beans interferes with the synthesis or translocation of auxin which normally prevents an abscission layer from forming.

Plant resistance to tarnished plant bug has been observed in several crop species, including cotton, alfalfa, beans and carrots, but with the exception of cotton and alfalfa, diverse sources of resistance are unknown (Tingey, 1976). According to Smith (1989) plant resistance to insects is composed of genetically inherited qualities that result in a plant of one cultivar or species being less damaged than a susceptible plant which lacks these qualities. This may take the form of one or more categories as defined by Painter

(1968): antibiosis, when plant directly interferes with the health of an insect; antixenosis, when a plant has some undesirable characteristic which encourages an insect to select an alternate host; and tolerance, when a plant has the ability to withstand or recover from insect damage. In practice, it may be very difficult to delineate between these categories, because they are not always biologically discrete entities, and frequently overlap (Smith, 1989).

In cotton, resistance to tarnished plant bug damage has been related to three morphological characteristics, including the size and shape of the floral bracts, the presence of epidermal pigment-bearing glands and a lack of nectar secretion. Inhibition of egg laying, reduced nymphal growth and survival, and reduced adult weights have been observed in other *Gossypium* species and may be used to develop resistance in cotton. The alfalfa cultivar 'Grimm' was observed to flower despite *Lygus* feeding, suggesting plant tolerance. Reduced adult *Lygus* survival has been noted on certain carrot cultivars, and reduced egg laying was observed on certain bean cultivars. Despite these examples, Tingey (1976) noted that our knowledge of plant resistance to *Lygus* and the factors mediating it is inadequate and deserves greater attention.

Strawberries and *Lygus*

Tarnished plant bug feeding is known to cause a distinctive malformation of strawberries. The apical end of the receptacle does not develop, resulting in concentration of achenes described as "apical seediness" (Schaefers, 1966). Such fruit, commonly referred to as "buttons", are unmarketable and may constitute a large percentage of the total harvest in a field when tarnished plant bug populations are high (Parker et al., 1978). Schaefers (1966) credits Forbes (1884) with first reporting the connection between tarnished plant bug feeding and strawberry malformation. Support for this observation followed and control measures, including the elimination of alternate hosts (Haseman, 1928) and pesticide applications (Mundinger, 1955), were recommended.

Research regarding tarnished plant bug on strawberry has concentrated on the effectiveness of chemicals for reducing damage (Howitt et al., 1965; Mundinger, 1955; Schaefers, 1966, 1972). Little has been done to determine the cause of the characteristic injury. Research involving a similar species, *L. hesperus* Knight, more common in the western United States, found that achenes on symptomatic strawberries were hollow, suggesting that these were the actual feeding sites. It was proposed that the feeding occurred after pollination, because the achenes were well developed, although hollow, and that the damage results from blocking growth stimulation of the receptacle (Allen and Gaede, 1963). This hypothesis was adopted for tarnished plant bug (Schaefers, 1980) although it has not been supported by observations of tarnished plant bugs actually feeding on achenes. In a more recent study, Riggs (1990) described *L. hesperus* feeding on strawberry and reported that achenes were the primary feeding sites.

Tarnished plant bugs are known to feed preferentially on developing seeds, including dill, parsnip, beet, beans, alfalfa, and guayule, and may cause these seeds to be hollow (Flemion et al., 1954; Hills & Taylor, 1948; Romney et al., 1945; Shull, 1933; Young, 1986). However, hollow achenes on strawberries are not necessarily indicative of tarnished plant bug feeding. Darrow (1966) stated that hollow yet full-sized achenes, can result from frost following pollination, and Schaefers (1966) noted that hollow achenes occur on berries showing no malformation. Damage due to tarnished plant bug may be a result of feeding on receptacle tissue. The destruction of this tissue by laceration and digestive enzymes could render it unable to enlarge despite a stimulus from the achenes.

The effect of flower development stage on strawberry malformation due to tarnished plant bug is unknown. Allen and Gaede (1963) stated that, for *L. hesperus*, feeding generally occurred between anthesis and the completion of achene enlargement, this being the period when the achenes were most accessible and easily penetrated. Malformation was observed most often when feeding occurred immediately after petal fall. However, tarnished plant bugs have been observed feeding upon strawberry receptacle tissue on nearly ripe fruit (Dill and Handley, unpublished). Feeding sites may change as berries develop, achenes being favored early, and receptacle tissue being preferred later, as the achenes become lignified. This change in sites, in turn, may affect the degree and character of any malformation. Riggs (1990) reported malformation from *L. hesperus* feeding one to two days after anthesis, but no damage was observed from feeding on five-day-old receptacles.

The amount of feeding injury required to cause apical seediness in strawberry is not known. Flemion et al. (1954) observed a large amount of mechanical damage to plant tissue during a single feeding by tarnished plant bugs. Others believe that tissue damage is primarily caused by enzymatic action of the saliva (Smith, 1920; Strong, 1970;

Varis, 1972). If the latter is true, saliva would have to be readily and rapidly transported beyond the initial feeding site or repeated feedings would be necessary to cause extensive damage. In greenhouse experiments, Allen and Gaede (1963) observed malformation from *L. hesperus* after a 24 hour exposure period. Riggs (1990) reported apical seediness from *L. hesperus* after a 48 hour exposure period. Parker et al. (1978) observed malformation from tarnished plant bugs following a 48 hour exposure period.

Resistance to tarnished plant bugs in strawberries has not been reported. Differences in damage levels have been observed among cultivars, but this has not been studied in detail (Schaefers, personal communication). Allen and Gaede (1963) stated that "striking differences" in the amount of injury were evident among different cultivars in a single field. However, they did not offer supporting data or mention what cultivars were present. Parker et al. (1978) stated that tarnished plant bugs can reduce strawberry yield by 10 to 60%, depending on cultivar, but no elaboration was made. Resistance to other arthropod species has been found in strawberries, including aphids (Barritt and Shanks, 1980), root weevils (Shanks et al., 1984) and mites (Kishaba et al., 1972; Shanks and Barritt, 1980), and breeding programs have sought to enhance this resistance. Resistance to tarnished plant bug has been observed and bred for in other crops, including cotton and alfalfa (Bailey, 1986; Lindquist et al., 1967; Tingey, 1976).

Tarnished plant bugs on strawberries are presently controlled with two to four insecticide cover sprays applied from prebloom to petal fall. Materials of choice include endosulfan, azinphos-methyl and malathion (Schloemann, 1992). Action (spray) thresholds for tarnished plant bugs in strawberries have been established, based on sampling the population in a field by shaking randomly selected flower clusters over a plate and counting the number of nymphs observed. The total number of nymphs is divided by the number of samples to determine the sample population. If the population exceeds the threshold, a spray is recommended (Schaefers, 1980, 1981). Research in Quebec (Mailloux and Bostanian, 1988, 1989) has found that an action threshold of only 0.10 to 0.25 nymphs per flower cluster should be used. A sequential sampling plan was developed to reduce the time required for sampling insect populations. Neither the action thresholds nor sequential sampling have been adequately field tested in the northeastern United States and have not yet been adopted by farmers.

CHAPTER II

STRAWBERRY FRUIT DEVELOPMENT AND THE EFFECTS OF FEEDING BY THE TARNISHED PLANT BUG (*LYGUS LINEOLARIS*)[1]

Introduction

Strawberry Fruit Development

The cultivated strawberry, *Fragaria ananassa* Duchesne, produces an aggregate fruit comprised of achenes arranged in a spiral fashion on an enlarged receptacle (Winton, 1902). The achenes are the true fruits of the strawberry, each containing a single embryo; however the fleshy receptacle forms the edible part of the berry. Growth of the receptacle is principally a function of cell enlargement in its cortex and pith. Cell division accounts for only 15 to 20 percent of the total growth, occurring mostly prior to anthesis, (Havis, 1943).

Webb et al. (1978) and others (Abbott et al., 1970; Moore et al., 1970) observed that strawberry fruit size and shape are functions of the number of achenes on a receptacle, the area of receptacle tissue surrounding each achene, and the positions of the achenes on the receptacle. Berries with fewer achenes will be smaller, as is the case for

[1]Published in The Strawberry into the 21st Century. A. Dale and J. J. Luby (eds.). Timber Press, Portland, OR. 1991.

fruit lower on the inflorescence, and berries which have more receptacle growth per achene will be larger. Arrangement of the achenes on the receptacle will affect distribution of growth, and therefore, berry shape.

Development of the receptacle is controlled by plant growth substances. Following fertilization, auxin is synthesized in the achenes and moves into the receptacle tissue, stimulating cell enlargement (Archbold and Dennis, 1985; Lis et al., 1978; Nitsch, 1950; Southwick and Poovaiah, 1987). Achenes produce auxin only if fertilized. Development of strawberry receptacles without fertilized achenes has been induced by exogenous auxin applications, but success has been limited (Archbold and Dennis, 1985; Mudge et al., 1981; Nitsch, 1950; Thompson, 1969; Tukey, 1952). Such experiments have shown that growth of unfertilized strawberries can be stimulated by auxins if the latter are applied within a limited period following anthesis and within a limited range of concentrations, and if no serious damage is done to the fruit structures, as, for example, removal of the carpels.

The Tarnished Plant Bug (*Lygus lineolaris* Palisot de Beauvois)

The tarnished plant bug undergoes three major life stages: egg, nymph, and adult. Eggs are approximately 1 mm long and flask shaped, and are typically inserted in plant stems just below the surface. Nymphs undergo five instars before becoming adults. The first instar is approximately 1 mm in length, and may vary in color from yellow to dark green. As each instar proceeds, size increases and wing pads develop. Adults are approximately 5 mm long and 3 mm wide. Color can vary greatly, ranging from yellow-brown to nearly black, with more or less distinct lines along the head and thorax (Brittain and Saunders, 1918; Crosby and Leonard, 1914; Kelton, 1975).

The preferred feeding sites for the tarnished plant bug appear to be meristematic tissues and developing flowers and fruit (Crosby and Leonard, 1914; Tingey and Pillemer, 1977; Young, 1986). The type of damage caused by phytophagous *Lygus* species as categorized by Tingey and Pillemer (1977) includes: localized wilting and necrosis, abscission of fruiting forms, morphological deformation of fruit and seed, altered vegetative growth, and tissue malformations. These species feed by the "lacerate and flush" method (Miles, 1972). Fine stylets are inserted into the plant tissue and penetrate both inter- and intracellularly. Repeated plunging of the stylets during feeding may render considerable mechanical damage to the tissue (Flemion et al., 1954). In addition, enzymes such as pectinase may be injected into the tissue via saliva, causing further cellular breakdown (Miles, 1972; Smith, 1920; Strong 1970; Varis, 1972).

The host range of the tarnished plant bug is extremely wide. Young (1986) lists 385 plant hosts, including at least 130 economically important species, and 21 of the 30 most important crops in the United States. Young suggests that the tarnished plant bug has the broadest documented feeding niche of any arthropod. According to Kelton (1975) the distribution of the tarnished plant bug includes all of the agricultural regions of North America. Young (1986) suggests that reports of areas with no known plant hosts may indicate a lack of research rather than the absence of the tarnished plant bug.

Fruit Malformation in the Strawberry

Strawberry fruit malformation can be caused by damage to the developing receptacle tissues or achenes, or by a lack of pollination. In the latter case, unpollinated achenes will not develop and synthesize auxins required to stimulate receptacle growth (Gilbert and Breen, 1987).

Tarnished plant bugs are known to cause a distinctive concentration of achenes at the apical end of strawberry receptacles, with an accompanying lack of development. Such fruit, called "nubbins" or "buttons," may constitute a large percentage of the total fruit when tarnished plant bug populations are high (Parker et al. 1978; Schaefers, 1966, 1980). Why this characteristic damage occurs is not well understood. Investigations carried out with *Lygus hesperus* Knight (Allen and Gaede, 1963) determined that achenes on symptomatic fruit were hollow, suggesting that these were the actual feeding sites. This conclusion was supported by subsequent studies of the tarnished plant bug (Schaefers, 1966). These findings would suggest that feeding by the tarnished plant bug occurs after pollination, as the achenes were well developed, even though hollow, and that the fruit damage is a result of the inability of affected achenes to supply the receptacle with auxin (Schaefers, 1980). There have been no observations of tarnished plant bugs actually inserting stylets into achenes, however, and Schaefers (1980) has noted a lack of detailed study on the nature of tarnished plant bug feeding on strawberries.

Tarnished plant bugs are known to feed preferentially on developing seeds, including dill, parsnip, beet, beans, alfalfa, and guayule, and may cause these seeds to be hollow (Flemion et al., 1954; Hills and Taylor, 1948; Romney et al., 1945; Shull, 1933; Young, 1986). However, hollow achenes in strawberries do not necessarily indicate tarnished plant bug feeding. Darrow (1966) states that hollow, yet full-sized, achenes can result from frost following pollination, and Schaefers (1966) notes that hollow achenes occur on berries showing no malformation. It is possible that the damage caused by the tarnished plant bug could be a result of feeding on the receptacle tissue. The destruction of this tissue by laceration and digestive enzymes could render it unable to grow despite an auxin stimulus from the achenes.

It is unclear what effect, if any, the stage of strawberry flower development has upon the degree of damage incurred as a result of tarnished plant bug feeding. Allen and Gaede (1963) state that, for *Lygus hesperus*, feeding generally occurs between anthesis and petal fall, this being the period when the achenes are most accessible and easily penetrated. However, tarnished plant bugs have been observed feeding on strawberry receptacle tissue on well-developed fruit (Dill and Handley unpublished). Feeding preferences may possibly change as berries develop, young achenes being favored early, and receptacle tissue being preferred later when the achenes have lignified.

It is not known if the characteristic tarnished plant bug damage to strawberry fruit is caused by a single feeding episode, or prolonged and/or repeated feedings. Flemion et al. (1954) observed a large amount of mechanical damage to plant tissue in a single feeding by tarnished plant bugs, but others believe that tissue damage is primarily caused by enzymatic action of the saliva (Smith, 1920; Strong, 1970; Varis, 1972). If the latter is true, more than one feeding may be necessary to cause extensive damage unless the saliva is readily and rapidly transported beyond the initial feeding site. Varis (1972) noted that piercing sugar-beet tissue with a fine needle and applying pectinase resulted in symptoms more like *Lygus* feeding than did piercing alone. It is questionable, however, whether the amount of damage done by simple piercing was comparable to that caused by the extensive stylet thrusting observed by Flemion et al. (1954). Some differences in tarnished plant bug damage have been observed among different strawberry cultivars, but this has not been studied in detail (Schaefers, personal communication). No strawberry cultivars have been cited as having resistance to the tarnished plant bug, but other crops, such as cotton and alfalfa, are known to possess characteristics which can be used in breeding to reduce tarnished plant bug damage (Bailey, 1986; Lindquist et al., 1967).

A better understanding of tarnished plant bug feeding behavior on strawberry and the subsequent malformation of the fruit may present new strategies for the management of this pest. Greenhouse studies were designed to determine the effects of fruit development stage, duration of tarnished plant bug feeding, and differences in susceptibility among different cultivars on strawberry malformation.

Materials and Methods

All plants were grown from dormant crowns planted in 6 inch pots filled with "Rediearth" peat-vermiculite mix. Plants were grown under natural light in a greenhouse with 26°C day temperature and 16°C night temperature. Primary blossoms were removed. Secondary blossoms were hand-pollinated at anthesis. Tarnished plant bugs were field-collected and starved for 24 hours prior to isolation with strawberry blossoms.

Effect of the Tarnished Plant Bug at Different Fruit Stages

Strawberry flowers (cultivar 'Mic Mac') were exposed to an adult tarnished plant bug for 48 hours at one of the following stages: (1) prebloom; (2) anthesis; (3) petal fall; (4) achene separation; and (5) pink receptacle. A control group was not exposed to tarnished plant bugs.

The pots were laid out in a randomized complete block design with 8 replications. Two secondary blossoms were treated per pot, unless fewer blossoms developed. Each tarnished plant bug was placed in a small plastic cage, into which a blossom was inserted with a foam stopper, slitted to act as a collar around the pedicel. Fruits were harvested when the receptacle tissue was fully red, or about 25 days after anthesis, and classified as normal, deformed, demonstrating apical seediness, or dead.

Effects of Feeding Duration of the Tarnished Plant Bug

Immediately following hand-pollination, small plastic cages were fitted over the secondary blossoms of 'Honeoye' and 'Redchief' strawberry plants. An adult tarnished plant bug was introduced into each cage for one of the following time periods: (1) 8 hours; (2) 24 hours; (3) 48 hours; (4) until harvest (about 25 days). Control blossoms were also placed in cages at anthesis, but no tarnished plant bug was introduced. Cages remained on the flowers throughout fruit development for all treatments.

The experiment was a factorial (2 cultivars x 5 time periods). Treatments were assigned to pots and laid out as a randomized complete block with 4 replications. Two secondary blossoms were treated per pot, unless fewer developed.

Fruit were harvested when the receptacle tissue was fully red or approximately 25 days after anthesis, and classified as normal, deformed, demonstrating apical seediness, or dead.

After grading, the fruits were crushed on a paper towel and allowed to dry. The achenes were then collected, placed in a centrifuge tube filled with distilled water and 0.1% Tween 20, and spun for 1 minute. The number of achenes which remained floating after centrifuging were counted and labelled nonviable. Samples of floating achenes examined under a microscope were nearly hollow with shriveled remains of cotyledons, while achenes that sank during the centrifuge treatment had plump cotyledons.

Results

Effect of the Tarnished Plant Bug at Different Fruit Stages

Tarnished plant bugs were observed feeding on all the stages of strawberry fruit to which they were exposed, but response to this feeding differed. Blossom death occurred in all cases when exposure to the tarnished plant bug occurred prebloom, and in all but one case when exposure occurred at anthesis (Table 2.1). Blossom death was also prevalent when tarnished plant bug exposure occurred at petal fall (67%). No death was observed during the achene separation or pink receptacle stages. Apical seediness was observed only when feeding occurred at petal fall, or in one case, at achene separation. Other deformities were most common at achene separation and the pink receptacle stage. Normal fruit development occurred most often in the controls, but was also observed when feeding occurred at the pink receptacle stage, and in one case at achene separation, but not when feeding occurred in the earlier developmental stages.

Single cases of fruit deformity, apical seediness and blossom death were observed in the control. It is not known if these resulted from poor pollination, a stray tarnished plant bug, or some other cause.

Effects of Feeding Duration of the Tarnished Plant Bug

Strawberry response to the tarnished plant bug varied according to exposure time (Table 2.2). Low exposure durations (8 to 24 hours) resulted in slight deformities or, less often, no visible deformities. Forty-eight hour exposure to the tarnished plant bug resulted in the highest proportion of apical seediness, the damage most often attributed to tarnished plant bug feeding, but also caused other deformities and blossom death. Continuous exposure to the tarnished plant bug following anthesis usually caused blossom death, but also resulted in a small proportion of apical seediness.

There appeared to be some difference in response to the tarnished plant bug based on cultivar. 'Honeoye' showed a lower proportion of deformed fruit at 8 and 24 hours than did 'Redchief', and a lower proportion of apical seediness at 48 hours. However, 'Honeoye' showed a higher degree of blossom death at 48 hours. Response to continuous exposure was similar for the cultivars.

Increasing exposure time to the tarnished plant bug greatly increased the percentage of nonviable achenes on strawberries (Table 2.3). Although a small number of nonviable achenes were noted in the controls, the percentage increased with each increase in tarnished plant bug exposure time. The greatest increases occurred between 24 and 48 hours and between 48 hours and continuous exposure. Blossoms with no receptacle development (classified as dead) had the highest percentage of nonviable achenes (80 to 90%), followed by those classified under apical seediness, other deformities, and finally, normal development.

Discussion

Effect of the Tarnished Plant Bug at Different Fruit Stages

Growth of strawberry receptacle tissue following anthesis is primarily a function of cell expansion in the cortex. This experiment suggests that tarnished plant bug feeding interferes with this process. Feeding at early blossom stages prevents cell expansion from occurring, resulting in no receptacle development. After cell expansion has begun --that is, during petal fall and achene separation-- tarnished plant bug feeding inhibits only some cells, while others develop normally. This damage results in receptacle deformation, the exact expression of which depends on the number and location of the affected cells. Apical seediness is a severe example of such damage, where only cells around the basal portion of the receptacle are fully expanded. Tarnished plant bug feeding at the pink receptacle stage causes little visible deformity because cell expansion is nearly complete.

Although tarnished plant bugs fed on strawberry blossoms at all stages, apical seediness, the deformity most commonly associated with the tarnished plant bug, was observed only after feeding at a relatively specific stage, and then was observed to occur inconsistently. Blossom death or other deformities were much more common. These types of damage may not occur to a significant degree under field conditions, due to the timing of flower development in relation to the emergence of the tarnished plant bug from overwintering; or perhaps such damage is attributable to other causes, such as poor pollination.

Effects of Feeding Duration of the Tarnished Plant Bug

The type and degree of deformation to strawberries caused by the tarnished plant bug is related to the duration of exposure. Isolation with a tarnished plant bug for as little as 8 hours caused visible deformation, but apical seediness, considered characteristic of tarnished plant bug feeding, occurred only after feeding durations of 48 hours or longer. Continuous exposure to the tarnished plant bug usually resulted in blossom death, which has not been attributed to the tarnished plant bug in the field.

The difference in cultivar response to the tarnished plant bug suggests that cultivars which appear to be less susceptible to the tarnished plant bug than others may simply express the injury differently. For example, in the field, 'Honeoye' may appear to be less susceptible to the tarnished plant bug, because fewer fruits show apical seediness, when in fact an equal or greater number of fruits are lost by blossom death, which is not typically considered.

Strawberry deformity was also associated with the viability of achenes. Increasing exposure to the tarnished plant bug caused a higher percentage of nonviable achenes. If the achenes are the primary feeding sites for the tarnished plant bug, their destruction results in poor growth of the receptacle tissue. Alternatively, if the receptacle tissue is the primary feeding site, its destruction may cause the loss of nutrient support to the achenes, leading to nonviability. The question of which flower parts serve as primary feeding sites for the tarnished plant bug is now under investigation.

Table 2.1 Condition of 'Mic Mac' strawberries exposed to tarnished plant bug for 48 hours at different stages of fruit development.

	Number of fruit			
Fruit stage	Normal	Deformed	Apical Seediness	Dead
Prebloom	0	0	0	5
Anthesis	0	1	0	5
Petal fall	0	0	2	4
Achene separation	1	3	1	0
Pink receptacle	2	1	0	0
Control	4	1	1	1

Table 2.2. Effect of increasing exposure to tarnished plant bug at anthesis on 'Honeoye' and 'Redchief' strawberries.

	Number of Fruit			
Feeding duration of tarnished plant bug	Normal	Deformed	Apical Seediness	Dead
		'Honeoye'		
Control	5	0	0	1
8 hours	2	4	0	0
24 hours	4	4	0	0
48 hours	0	1	1	4
Anthesis-Harvest	0	0	1	7
		'Redchief'		
Control	4	2	0	0
8 hours	0	5	0	1
24 hours	1	7	0	0
48 hours	0	3	3	0
Anthesis-harvest	0	0	1	6

Table 2.3. Effect of increasing tarnished plant bug exposure at anthesis on subsequent achene viability of 'Honeoye' and 'Redchief' strawberries.

	Percentage of nonviable achenes per strawberry	
Feeding duration of tarnished plant bug	'Honeoye'	'Redchief'
Control	9.7	15.4
8 hours	13.0	17.4
24 hours	16.6	24.3
48 hours	60.3	58.1
Anthesis-harvest	90.4	79.9

CHAPTER III

A MICROSCOPIC EXAMINATION OF TARNISHED PLANT BUG (HETEROPTERA: MIRIDAE) FEEDING DAMAGE TO STRAWBERRY[2]

Abstract

Light and scanning electron microscopy were used to assess feeding damage caused by tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), to strawberries (*Fragaria x ananassa* Duchesne). Holes found in strawberry achenes after feeding were consistent with the size and shape of tarnished plant bug stylets. Insects observed while feeding during early fruit development stages (i.e., anthesis to petal fall) repeatedly penetrated achenes with their stylets. In later stages of fruit development, feeding sites changed to receptacle tissue, although usually near an achene. Achene injury during early fruit development stages is the most likely cause of the apical seediness malformation commonly associated with tarnished plant bug. Feeding during later developmental stages probably results in more localized damage, including creases and indentations.

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Introduction

The tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), is a serious pest of strawberries in central and northeastern North America. This insect causes a distinctive malformation of strawberries, described as apical seediness (Fig. 3.1). Such fruit, called "buttons," are usually unmarketable and may constitute a large percentage of the total harvest when tarnished plant bug populations are high (Schaefers, 1966, 1980; Parker et al., 1978).

The strawberry (*Fragaria x ananassa* Duchesne) is an aggregate fruit with numerous achenes ("seeds") arranged in a spiral pattern on a swollen, fleshy receptacle, which forms the edible part of the berry. Growth of the receptacle from anthesis to harvest is a function of cell enlargement, which is in part controlled by plant hormones. After pollination, the hormone indoleacetic acid is synthesized in the achenes and translocated to the receptacle, where it stimulates cell enlargement (Nitsch, 1950; Lis et al., 1978; Archbold & Dennis, 1985; Southwick and Poovaiah, 1987).

Although there has been little research regarding tarnished plant bug feeding behavior on strawberries, studies with a similar species, *Lygus hesperus* Knight, more common in western North America, have shown that many achenes on symptomatic strawberries were hollow, suggesting that these were the likely feeding sites (Allen and Gaede, 1963). Handley (1991) observed that strawberries showing apical seediness after tarnished plant bug feeding had a high percentage of hollow achenes. However, hollow achenes on strawberries are not necessarily indicative of tarnished plant bug feeding. Hollow achenes are known to occur on strawberries showing no deformities (Schaefers,

1966) and may be caused by frost injury (Darrow, 1966). More recently, Riggs (1990) described *L. hesperus* feeding behavior on strawberry flowers and reported damage to individual achenes. Schaefers (1966, 1980) suggested a similar feeding behavior for tarnished plant bug, but noted a lack of documented support. In the study reported here we used light and scanning electron microscopy to closely examine the feeding behavior of tarnished plant bug on strawberry blossoms and determine the cause of the characteristic injury on the fruit.

Materials and Methods

Strawberry flowers were harvested from greenhouse-grown 'Tribute' plants during 1989 and 1990. Fresh flowers were placed individually in 60 by 20 mm petri dishes. Tarnished plant bugs collected from the field or reared on potato sprouts (Slaymaker and Tugwell, 1982), were starved for 24 h, and then placed in petri dishes with the flowers. The dishes were placed under a dissecting microscope (Olympus model SZTr) to observe and photograph feeding behavior. Twenty insects were studied in detail and photographed while feeding. The sample included adult and immature stages of tarnished plant bugs, which were exposed to strawberry blossoms ranging in development from anthesis to fully ripe.

To observe feeding with the scanning electron microscope, a dissecting needle was inserted into the side of the strawberry receptacle before the introduction of the insect into the petri dish. Once feeding was observed through the dissecting microscope, the receptacle and bug were gently lifted from the petri dish with the dissecting needle and rapidly dipped into liquid nitrogen, freezing the bugs in place. Frozen samples were immediately placed in chilled 50% alcohol, then run through an alcohol dehydration series (50 - 100% ethanol) and critical point drying (Sass, 1951). The samples were mounted on stubs and sputter-coated with gold palladium for examination with the scanning electron microscope (Amray AMR 1000).

To locate sites of feeding injury on flowers, starved tarnished plant bugs were isolated on single flowers in small plastic cages and were allowed to feed during a 48-h period. Flowers were then harvested and fixed in FAA solution (Sass, 1951). They were run through an alcohol dehydration series and critical point drying before being mounted and coated with gold palladium for scanning electron microscopy.

To photograph tarnished plant bug mouthparts, bugs were killed in ethyl acetate, thoroughly air-dried, then directly mounted on stubs and coated with gold palladium for scanning electron microscopy.

Results

Tarnished plant bugs readily fed upon the strawberry blossoms with which they were isolated. Under the dissecting microscope, achenes were observed to be the primary feeding sites on flowers between anthesis and petal fall (Fig. 3.2). Achenes that had been fed upon became discolored shortly thereafter, indicating that considerable damage had occurred. Once receptacle enlargement had begun, the insect's preferred feeding site changed from the achenes to the receptacle, although these sites were always close to an achene (Fig. 3.3). The insects repeatedly probed numerous sites before prolonged feeding episodes were initiated. The observed feeding behavior of adult and immature tarnished plant bugs was similar, although the nymphs seemed to seek and exploit feeding sites more rapidly, making them better subjects for this study.

Scanning electron microscopy revealed small holes in the achenes fed upon by tarnished plant bug (Fig. 3.4). The stylets of the tarnished plant bug appeared to be fine and pointed, with sharp serrations angled back toward the head, and well suited for penetrating and lacerating plant tissues (Fig. 3.5). Under high magnification (1000 x), the size of the holes in the achenes was consistent with the size of tarnished plant bug stylets.

Under the scanning electron microscope, a tarnished plant bug feeding at anthesis was found to have its stylets embedded in the side of an achene (Fig. 3.6). A bug feeding on a slightly more mature blossom was found to have its stylet embedded in receptacle tissue (Fig. 3.7). The cells surrounding the stylet appeared to be collapsing as a result of the feeding.

Discussion

Tarnished plant bugs are known to feed primarily on meristematic tissues and developing flowers of the many host plants they infest (Tingey and Pillemer, 1977; Young, 1986). Miles (1972) described the feeding technique as "lacerate and flush." Observed feeding behavior of the tarnished plant bug included penetration of tissue at a feeding site and repeated plunging of the stylets through it. Digesting enzymes, including pectinase, have been isolated from tarnished plant bug saliva and are known to be injected into the tissue. This causes further tissue breakdown (Flemion et al., 1954; Miles, 1972). The resulting damage may include localized tissue wilting and necrosis, fruit abscission, morphological deformation of the fruits and seeds, and altered growth and malformations of vegetative tissues (Tingey and Pillemer, 1977).

On strawberry, tarnished plant bug appears to feed preferentially upon developing achenes during the early fruit development stages (i.e., from anthesis to petal fall). Stylets were observed entering achenes repeatedly (Figs. 3.2 and 3.6) and appeared to cause considerable damage, as indicated by the discoloration that soon followed. This is similar to the observations of Flemion et al. (1954) on other plant tissues. The destruction of endosperm within achenes during this stage of development would curtail indoleacetic acid synthesis and its translocation to the receptacle. The receptacle tissue is unlikely to enlarge normally without a supply of this hormone (Nitsch, 1950). "Buttoning" typically associated with tarnished plant bug could develop as a result of consequent abnormal receptacle development as suggested by Allen and Gaede (1963) for *L. hesperus* on strawberry. Holes observed in the achenes after feeding by tarnished plant bug (Fig. 3.4) were consistent with the size and shape of the insect's stylets (Fig. 3.5), but did not match the damage to achenes described by Riggs (1990) for *L. hesperus*. Holes in the latter study appeared to be larger and less defined in shape.

The feeding sites of tarnished plant bug changed from the achenes to the receptacle as fruit development progressed. It is during the earlier stages of fruit development that the achenes are most accessible and easily penetrated. As development continues, the achenes enlarge and become increasingly lignified, making them more difficult for the stylets to penetrate. At the same time, the relatively soft receptacle tissue becomes more exposed. Feeding sites on the receptacle were nearly always very close to an achene (Figs. 3.3 and 3.7). Sites near achenes may be more attractive than other sites because of the vasculature and nutrient supply associated with the developing embryo in each achene.

Feeding on the receptacle tissue rather than achenes probably differs in its effect on fruit development. Rather than affecting a large area of tissue beyond the feeding site, as might occur when auxin synthesis and transport is disrupted, the effect would tend to be limited to the area directly damaged by the stylet and enzymes in the saliva. Although the injured cells could no longer enlarge in response to indoleacetic acid, overall fruit development would not be as seriously affected. Damage would be more localized as feeding occurred later in fruit development because tissue volume would be greater and a proportionately smaller number of cells would be affected. The overall damage from feeding on nearly mature fruit would be less extensive because cell enlargement, fruit size, and fruit shape are nearly complete. Previous studies have shown that the occurrence of apical seediness as a result of tarnished plant bug feeding decreases as fruit development progresses. Symptoms on later stages of fruit development were more or less noticeable indentations or creases in the receptacle (Handley, 1991). Other factors, including temperature (Bostanian et al., 1990) and cultivar (Handley et al., 1991), may play a role in the feeding behavior of tarnished plant bug on strawberries and may have an effect on consequent fruit malformation.

Figure 3.1. Apical seediness or "buttoning" malformation on strawberry attributed to tarnished plant bug feeding.

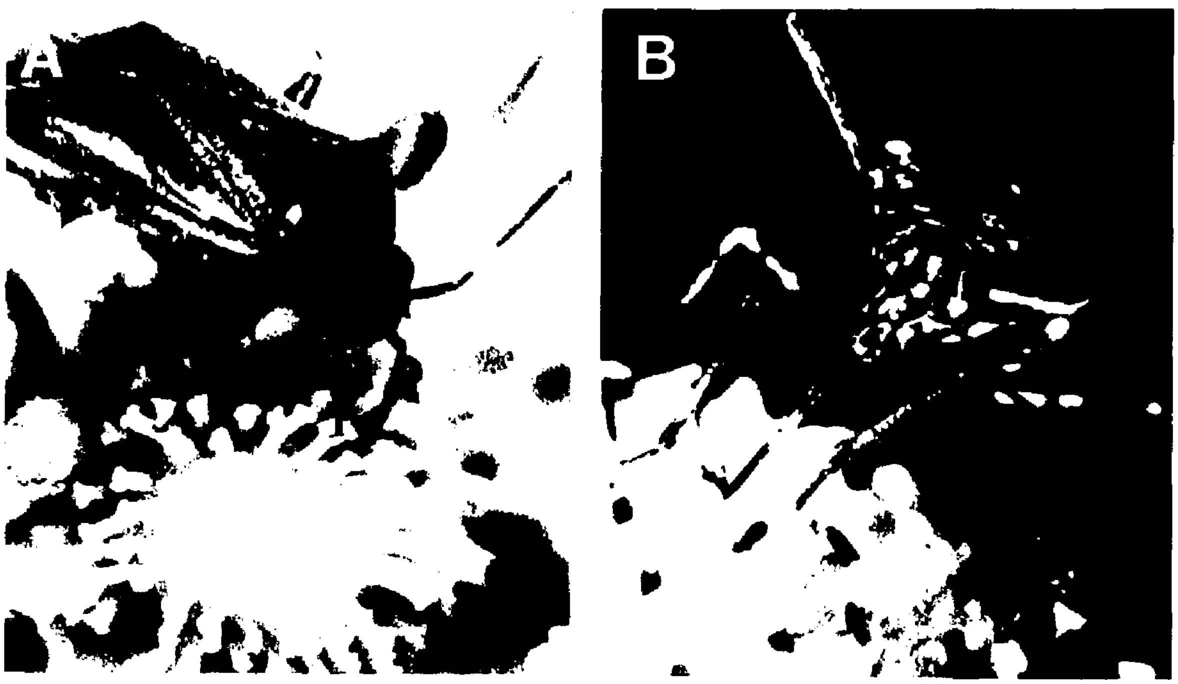

Figure 3.2. Tarnished plant bug feeding on achenes of strawberry flower at anthesis (A) and petal fall (B).

Figure 3.3. Tarnished plant bug feeding on strawberry receptacle tissue near achenes. (A) Nymph feeding at achene separation stage. (B) Adult feeding on mature tissue near achene in depressed "well" of receptacle.

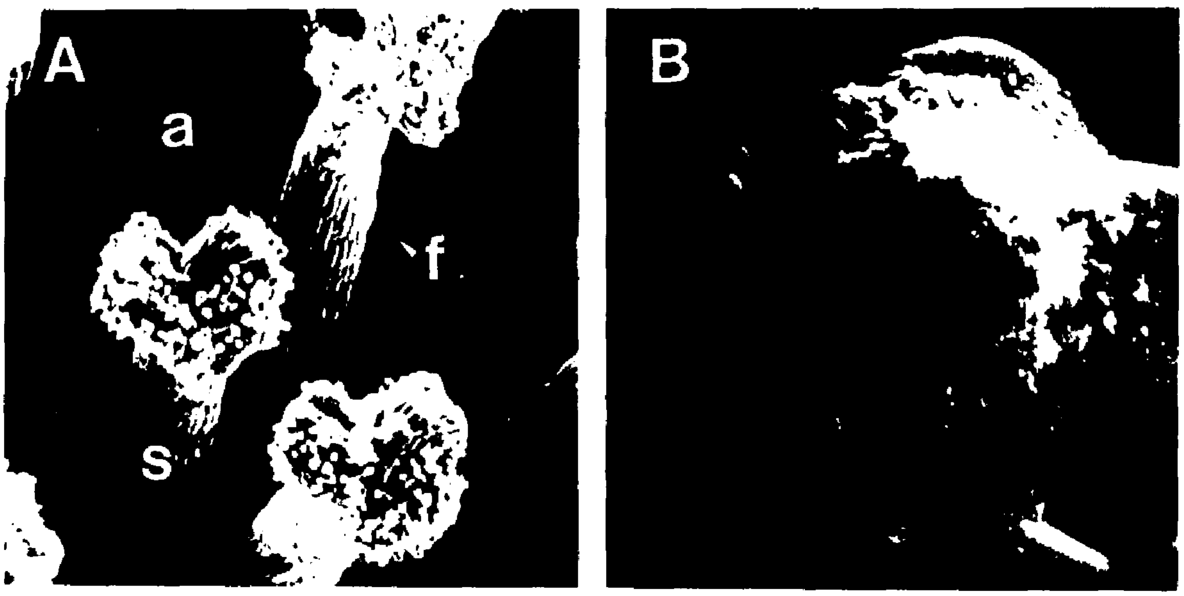

Figure 3.4. Feeding holes of tarnished plant bug in strawberry achenes, ~ 48 hours after anthesis. (A) 60 x, (B) 1,000 x (a, achene; f, feeding hole; s, style).

Figure 3.5. Stylet of tarnished plant bug, 1,000 x.

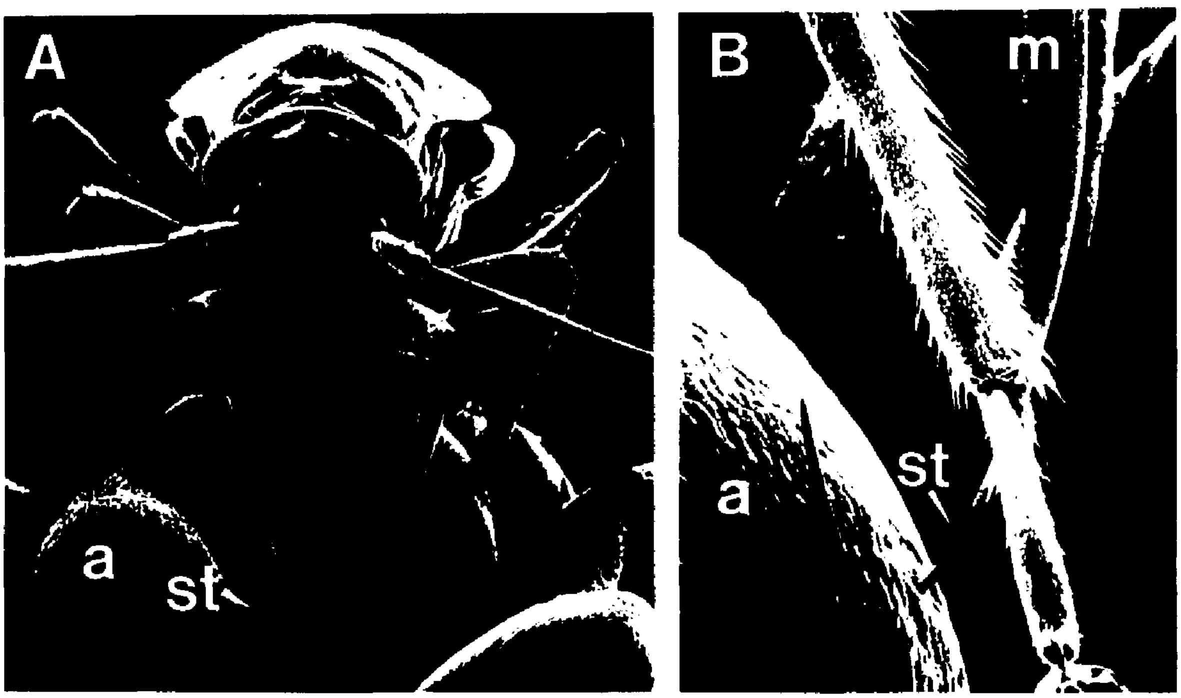

Figure 3.6. Tarnished plant bug feeding on strawberry with stylets entering side of achene. (A) 32 x, (B) 100 x (a, achene; st, stylet; m, rostrum).

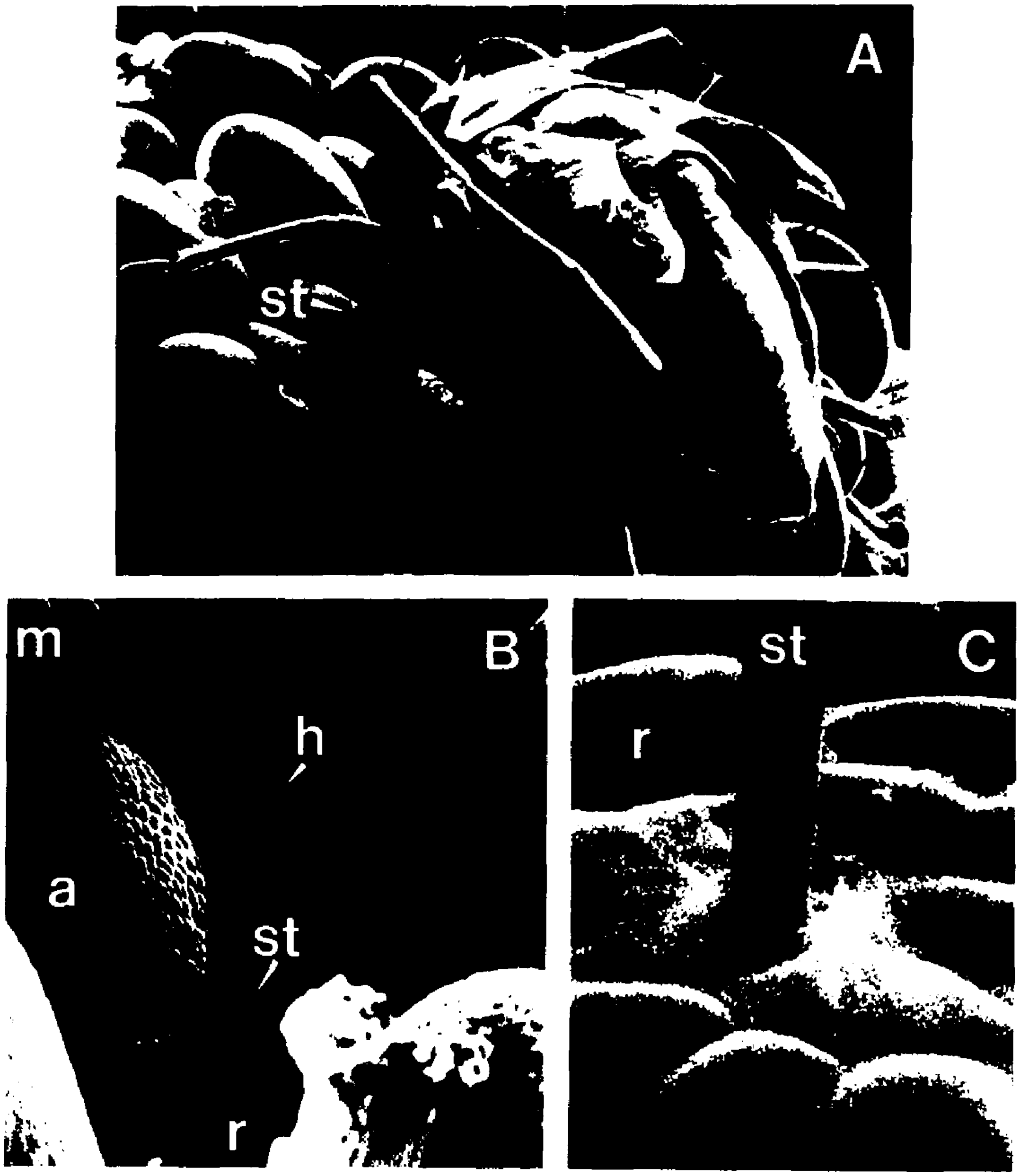

Figure 3.7. Tarnished plant bug feeding on strawberry with stylets in receptacle tissue. (A) 22 x; (B) 100 x; (C) 1,000 x (a, achene; r, receptacle; st, stylet; m, rostrum; h, epidermal hair).

CHAPTER IV

FIELD SUSCEPTIBILITY OF TWENTY STRAWBERRY CULTIVARS TO TARNISHED PLANT BUG INJURY[3]

Abstract

Twenty Junebearing strawberry cultivars grown in a matted row trial in Monmouth, Maine were evaluated for susceptibility to tarnished plant bug injury during the 1987 and 1988 harvest seasons. A wide range of injury was observed among cultivars. 'Honeoye', 'Sparkle', 'Veestar' and 'Canoga' had significantly less injury than other cultivars, as measured by number and weight of fruit showing apical seediness. 'Mic Mac', 'Scott', 'Blomidon' and 'Redchief' were most susceptible. Cultivars with the least injury tended to have the greatest marketable yields. Characteristics that might impart resistance were not obvious from this study, but there is some evidence that tarnished plant bug resistance could be selected for in breeding programs.

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[3]Scientific Contribution Number 1710 from the New Hampshire Agricultural Experiment Station. Published in Fruit Varieties Journal 45(3): 166-169. 1991.

Introduction

The tarnished plant bug, *Lygus lineolaris* P.de B. (Hemiptera: Miridae), is a serious strawberry pest in northeastern and midwestern North America. Both adult and immature (nymph) stages feed on strawberry flowers and fruit causing a distinctive malformation of the developing receptacle described as "apical seediness" (Schaefers, 1972), and commonly called "buttoning". Tarnished plant bugs feed on developing achenes and/or their supporting tissues, halting their importation of photosynthates and their exportation of auxins to the receptacles. Apical seediness is ascribed to impaired achene and receptacle tissue development (Allen and Gaede, 1963; Parker et al., 1978). There have been recent efforts to develop economic thresholds for tarnished plant bug in strawberries (Mailloux and Bostanian, 1989), but these have not yet been widely adopted by farmers. Most commercial strawberry fields receive two to five insecticide sprays each spring to prevent serious economic loss from tarnished plant bug injury.

Although resistance to tarnished plant bug has been observed and exploited in other crops, such as alfalfa and cotton (Tingey, 1976), there has been no published report of resistance in strawberry. This experiment reports on the differences observed in tarnished plant bug injury among 20 strawberry cultivars in a field trial over two harvest seasons.

Materials and Methods

A strawberry trial was established at the Agricultural Experiment Station in Monmouth, Maine, in the spring of 1985. Twenty cultivars were planted in a randomized complete block design with five replications. Plants were initially spaced 46 cm apart in rows 1.2 m apart. They were deblossomed and runners allowed to develop in matted rows 50 cm wide x 366 cm long. Fertilizers, herbicides and fungicides were applied according to regional recommendations (Pritts et al., 1987). Straw mulch for winter protection was applied each fall and removed the next spring. Following each harvest season the planting was renovated by mowing and rototilling rows to a 25 cm width.

In order to more closely represent conditions in a conventional strawberry field, all plots received insecticide sprays each spring to reduce populations of tarnished plant bug and strawberry bud weevil. In 1987, the plots were sprayed twice with endosulfan, once at bud stage and again at prebloom. In 1988 they were sprayed only once at prebloom with a tank mix of malathion and methoxychlor. In both seasons tarnished plant bugs were observed to be prevalent throughout the field during fruit development.

Tarnished plant bug injury to fruit was monitored in the planting during the 1987 and 1988 harvest seasons. Fruit was harvested from the center 2.7 m of each 3.7 m plot and divided into two grades: marketable and tarnished plant bug injured, the latter defined by apical seediness. Fruit losses from other causes, e.g. *Botrytis*, were negligible. Fruit from each plot and grade was counted and weighed. Tarnished plant bug injury was expressed as percentage of fruit number and fruit weight exhibiting apical seediness. Marketable fruit weight for each season was divided by marketable fruit number to determine mean fruit size. Means for percent tarnished plant bug injury by weight were adjusted by square root transformation. Duncan's Multiple Range Test was used to determine significant differences between means.

Results

Significant differences in tarnished plant bug injury, marketable yields and berry size were observed among cultivars in 1987 and 1988 (Tables 4.1, 4.2). 'Honeoye' had the lowest injury by weight and number during both years. 'Sparkle', 'Veestar', 'Annapolis' and 'Canoga' also had low injury. 'Kent', 'Mic mac', 'Scott', 'Blomidon' and 'Redchief' were highly susceptible to injury. 'Guardian' and 'Allstar' consistently fell into the middle range. 'Raritan', 'Earliglow', 'Redcoat', 'Glooscap', 'Cornwallis', 'Catskill', 'Surecrop', and 'Midway' were inconsistent over the two years.

'Honeoye' produced the highest marketable yields by weight and number over the combined harvest periods, followed closely by 'Sparkle' and 'Canoga'. 'Kent', 'Redcoat' and 'Catskill' had high yields in 1987, but much lower yields the following year. 'Veestar', 'Earliglow', 'Blomidon', 'Cornwallis', 'Mic Mac', and 'Allstar' had the lowest yields. The remaining cultivars fell into a middle range, not differing significantly from one another.

'Annapolis' fruit consistently was the largest, but also lowest in numbers. 'Allstar', 'Canoga', and 'Mic Mac' also had large fruit. 'Sparkle' and 'Veestar' consistently had the smallest fruit, followed by 'Redcoat', 'Earliglow', and 'Surecrop'.

There was a significant negative relationship between the amount of tarnished plant bug injury and marketable yield. Marketable yields were reduced by number ($r = -.63$)

and by weight ($r = -.52$) as tarnished plant bug injury increased. There was no significant relationship between injury and fruit size.

Discussion

Significant and consistent differences in tarnished plant bug injury were observed in this two year trial indicating resistance among the twenty cultivars studied. Cultivars such as 'Honeoye' and 'Sparkle' which were less susceptible to injury had consistently higher marketable yields than cultivars which were more susceptible, such as 'Mic Mac' and 'Blomidon'. 'Kent' was the exception, being both highly susceptible and relatively productive. This apparent anomaly may be explained by the large number of fruit produced by this cultivar.

Tarnished plant bug injury appeared greater when measured by fruit number rather than by weight. This is due to the injury being more prevalent on fruit developing later on the inflorescence, that is tertiary and quaternary fruit which tend to be smaller than primary and secondary fruit and thus weigh less regardless of injury. Despite this characteristic, cultivar susceptibility did not appear closely related to time of ripening. Some late ripening cultivars, such as 'Canoga' and 'Sparkle', had little injury, while some early ripening cultivars, such as 'Earliglow' and 'Cornwallis', had high injury levels. Therefore the differences observed in this trial are not simply attributable to the timing of insect activity with fruit development.

There is a possible genetic role in the range of susceptibility observed. 'Honeoye' and 'Canoga', which had low susceptibility to injury, both have 'Holiday' as a parent, which, in a nonreplicated trial, had the lowest injury of any cultivar studied (Handley and Dill, unpublished). 'Veestar', and its parent 'Sparkle', also had low susceptibility. 'Kent' and 'Mic Mac', both highly susceptible to injury, share 'Tioga' as a parent, and 'Cornwallis', for which 'Kent' was a parent, was also highly susceptible. 'Blomidon' however, which has 'Holiday' as a parent, was very susceptible, and 'Annapolis', which has 'Mic Mac' as a grandparent, was not very susceptible.

Plant resistance to insects can include avoidance, nonpreference, tolerance and antibiosis (Painter, 1968). The mechanisms may be anatomical, physiological, biochemical, or phenological. The differences observed in this study may be due to one or a combination of these factors. The fact that significant differences exist indicates that investigations of the mode(s) of resistance and further screening of strawberry germplasm could yield effective control mechanisms for this important pest.

Table 4.1. Tarnished plant bug injury as percent fruit weight (g) and percent fruit number (no.) of marketable yield and berry size of 20 strawberry cultivars in Monmouth, ME, 1987.[z]

Cultivar	% TPB injury (g)[y]	% TPB injury (no.)	Marketable fruit (no.)	Marketable fruit (g)	Berry size (g)
Honeoye	8.4 a	27.2 a	309 a	4084 a	14.1 bc
Sparkle	10.2 ab	27.1 a	305 a	2674 bc	8.8 d
Canoga	10.3 ab	33.6 ab	139 cd	2290 bcd	19.3 a
Redcoat	11.1 abc	26.9 a	322 a	3224 ab	10.1 cd
Catskill	12.3 abc	30.4 a	288 a	3071 ab	10.7 cd
Veestar	13.1 abc	30.4 a	160 bcd	1377 de	8.6 d
Annapolis	15.1 abcd	39.3 abcd	113 cd	1750 cde	16.0 ab
Surecrop	15.8 abcd	38.4 abcd	158 bcd	1621 cde	10.3 cd
Midway	16.2 bcde	34.5 abc	173 bc	1859 cde	10.7 cd
Guardian	16.4 cde	38.0 abcd	115 cd	1400 de	12.0 bcd
Allstar	17.3 cde	39.0 abcd	62 d	887 e	14.4 bc
Glooscap	18.3 cde	45.6 bcde	175 bc	1866 cde	11.2 cd
Scott	22.0 cdef	45.9 bcde	125 cd	1539 cde	12.3 bcd
Redchief	22.0 cdef	49.0 cde	169 bc	1857 cde	11.0 cd
Blomidon	23.1 def	47.8 bcde	101 cd	1141 de	11.7 bcd
Earliglow	24.7 ef	47.7 bcde	132 cd	1318 de	9.8 cd
Raritan	25.0 ef	52.1 de	103 cd	1085 e	10.6 cd
Cornwallis	28.0 ef	57.4 e	99 cd	1132 de	11.6 bcd
Mic Mac	28.0 ef	55.8 e	78 cd	1071 e	14.1 bc
Kent	29.2 f	52.3 de	252 ab	3195 ab	12.8 bcd

[z]Means followed by the same letter within columns do not differ significantly (Duncan's Multiple Range Test, $P = 0.05$).
[y]Means adjusted by square root transformation.

Table 4.2. Tarnished plant bug injury as percent fruit weight (g) and percent fruit number (no.) of marketable yield and berry size of 20 strawberry cultivars in Monmouth, ME, 1988.[z]

Cultivar	% TPB Injury (g)[y]	% TPB Injury (no.)	Marketable Fruit (no.)	Marketable Fruit (g)	Berry size (g)
Honeoye	7.7 a	22.3 a	337 b	3314 a	10.0 bcdef
Annapolis	8.1 a	26.6 ab	73 g	1150 efgh	15.4 a
Glooscap	12.1 ab	27.3 ab	316 b	2830 ab	9.1 cdef
Veestar	12.4 ab	31.0 abcd	103 efg	798 gh	7.8 fg
Sparkle	14.6 abc	25.7 ab	449 a	2926 ab	6.5 g
Canoga	14.7 abc	29.9 abc	219 c	2405 bc	11.1 bc
Raritan	19.0 bcd	38.1 bcde	191 cde	1572 defg	8.2 efg
Earliglow	20.2 bcde	44.5 cdefg	104 efg	934 efgh	9.1 cdef
Redcoat	20.5 bcde	39.9 bcdef	204 cd	1669 de	8.1 efg
Guardian	22.1 cde	46.2 defg	118 defg	1352 efgh	11.5 b
Allstar	22.1 cde	47.2 efg	71 g	1031 efgh	14.8 a
Cornwallis	22.4 cde	47.8 efg	111 efg	1060 efgh	9.6 bcdef
Blomidon	24.7 def	48.1 efg	86 g	934 efgh	11.0 bcd
Redchief	24.9 def	53.5 efg	136 cdefg	1353 efgh	10.3 bcde
Scott	25.7 def	49.6 efg	99 fg	996 efgh	10.1 bcdef
Catskill	27.0 def	45.6 defg	185 cdef	1593 def	8.8 def
Kent	27.6 def	44.4 cdefg	216 c	2091 cd	9.8 bcdef
Mic mac	29.9 def	54.9 fg	92 g	1069 efgh	11.7 b
Surecrop	31.8 ef	57.2 g	84 g	707 h	8.3 efg
Midway	34.8 f	55.5 fg	91 g	830 fgh	9.4 bcdef

[z]Means followed by the same letter within a column do not differ significantly (Duncan's Multiple Range Test, $P = 0.05$).
[y]Means adjusted by square root transformation.

CHAPTER V

TARNISHED PLANT BUG INJURY ON SIX STRAWBERRY CULTIVARS TREATED WITH DIFFERING NUMBERS OF INSECTICIDE SPRAYS[4]

Abstract

Six strawberry (*Fragaria x ananassa* Duchesne) cultivars known to vary in susceptibility to tarnished plant bug (*Lygus lineolaris* Palisot de Beauvois) injury (apical seediness) were grown for two seasons under three insecticide regimes (three sprays, one spray and no spray) to determine if differences in susceptibility could be used to modify chemical controls for this insect. The most susceptible cultivars harbored more nymphs than the least susceptible cultivars. Increased marketable yield as a result of insecticides was most pronounced on susceptible cultivars. Differences in injury among cultivars were greatest when no insecticide was applied. 'Honeoye' and 'Sparkle' had the least apical seediness, followed by 'Redchief', 'Guardian' and 'Kent'. 'Mic Mac' consistently had the highest level of injury. When insecticide applications were reduced, apical seediness did not increase significantly for cultivars exhibiting low susceptibility.

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Chemical name used: 0,0-dimethylphosphorodithioate of diethylmercaptosuccinate (malathion).

Introduction

Injury to strawberry fruit caused by tarnished plant bug (*Lygus lineolaris*) can result in serious economic loss to farmers in most regions of North America. This insect feeds on strawberry flowers and fruit causing a distinctive malformation of the fruit tissue described as "apical seediness" (Schaefers, 1966) and commonly called "buttoning" or "catfacing". As few as one tarnished plant bug per four flower clusters can cause significant economic loss in commercial fields (Mailloux and Bostanian, 1989; Schaefers, 1980). The feeding destroys developing achenes and/or their supporting tissues, disrupting the export of auxin from achenes to the receptacle. Apical seediness occurs because of impaired receptacle development (Allen and Gaede, 1963; Handley, 1991; Parker et al., 1978; Riggs, 1990).

Tarnished plant bug infestations in June-bearing strawberries are controlled almost exclusively through two to five insecticide applications from prebloom to petal fall (Schaefers, 1981). Integrated pest management techniques, including population monitoring, and the use of action thresholds and biological controls, have recently been suggested (Bostanian et al., 1990; Day et al., 1990; Mailloux and Bostanian, 1988; 1989), but have not been widely adopted by farmers. Genetic resistance offers potential for control. Resistance to tarnished plant bug has been observed in cotton and alfalfa and is now being exploited in breeding programs (Tingey, 1976). Recently, differences in damage from tarnished plant bug have been observed among strawberry cultivars, suggesting that some resistance may exist (Handley et al., 1991). The present study was initiated to evaluate how differences in susceptibility to injury among June-bearing strawberry cultivars may affect insecticidal control of tarnished plant bug.

Materials and Methods

Based on a previous evaluation of 16 strawberry cultivars for susceptibility to tarnished plant bug injury (Handley et al., 1991) six June-bearing strawberry cultivars were selected to reflect a range of vulnerability. The cultivars, from least to most susceptible, 'Honeoye', 'Sparkle', 'Redchief', 'Guardian', 'Kent' and 'Mic Mac,' were planted in narrow raised beds with ten plants spaced 15 cm apart in single rows, 1.5 m between rows, and 1.5 m between plots, at the Agricultural Experiment Station in Monmouth, Maine. All blossoms were removed during the planting year and runners were removed throughout the experiment. Straw mulch was applied to all plots for winter protection. Treatments were assigned to plots arranged in a split plot design in six replications with insecticide sprays as the main plots and cultivars as the subplots. For both harvest seasons, one third of the plots received sprays of malathion (0,0-dimethylphosphorodithioate of diethylmercaptosuccinate 50% at a rate of 7.9 ml per l water) at prebloom, early bloom and petal fall. One third of the plots received only the prebloom spray, and one third of the plots received no malathion. Tarnished plant bug nymphs were counted prior to the start of harvest by shaking two flower clusters per plot over a white plate and counting the fallen insects. Fruits were harvested, counted, weighed and placed into one of three grades: marketable; apical seediness, or other deformities. Tarnished plant bug injury was measured as percent weight of fruit exhibiting apical seediness. Data were subjected to analysis of variance. Means were adjusted by arcsine or square root transformations where necessary, and separated using Duncan's Multiple Range Test.

Results

Populations of nymphs were much higher during 1990 than 1991 (Table 5.1). Within cultivars, plots which received three applications of malathion had the lowest populations. Compared to no spray, a single spray did not significantly reduce nymph populations, except on 'Kent' in 1991. Differences among cultivars were most apparent during 1990 in plots not receiving malathion, although a similar trend was evident for each insecticide treatment. 'Honeoye' had the lowest number of nymphs, significantly fewer than on 'Guardian', 'Mic Mac' and 'Kent'.

Yields of marketable fruit differed significantly among cultivars and insecticide treatments in both years (Table 5.2). In unsprayed plots, all cultivars except 'Guardian' in 1990, and 'Sparkle' and 'Redchief' in 1991 had lower yields than plots receiving three sprays. A single spray improved yields consistently only for 'Honeoye'. When sprays were reduced from three to one, marketable yields declined for 'Kent', 'Mic Mac' and 'Sparkle' in 1990, and 'Kent', 'Mic Mac' and 'Guardian' in 1991. Reducing sprays did not affect yields of 'Honeoye', 'Redchief' or 'Guardian' in 1990, or of 'Honeoye', 'Sparkle' or 'Redchief' in 1991. 'Kent' had the highest yields under the three-spray treatment, but when no insecticide was applied, its yields were less than or equal to nearly all other cultivars. 'Honeoye' produced high yields when no malathion was applied, significantly higher than all other cultivars except 'Kent' and 'Redchief' in 1991.

Unsprayed plots had more tarnished plant bug injury than sprayed plots for all cultivars except 'Honeoye' in 1990 (Table 5.3). 'Honeoye' injury levels were not significantly affected by malathion sprays. There were fewer injured fruit in single spray plots than in unsprayed plots for 'Mic Mac' in 1990, and 'Mic Mac', 'Kent', 'Sparkle', and 'Guardian' in 1991. Three sprays compared to no spray reduced injury for all cultivars except 'Honeoye' and, compared to one spray, for all cultivars except 'Honeoye'(1990) and 'Kent', 'Honeoye' and 'Sparkle' (1991).

Differences in the amount of apical seediness among cultivars were diminished when malathion was applied. 'Honeoye' and 'Sparkle' had the lowest levels of injury when no malathion was applied. Injury to 'Honeoye' fruit in unsprayed plots was no greater than to fruit of other cultivars receiving three sprays. 'Mic Mac' had the highest level of injury of all cultivars in 1990. 'Kent', 'Redchief' and 'Guardian' also had high injury levels. In 1991, 'Mic Mac', 'Guardian' and 'Kent' had the highest injury levels.

Fruit deformities other than apical seediness, such as creasing and puckering, tended to be greatest on 'Honeoye' and 'Sparkle', the two cultivars which had the lowest levels of tarnished plant bug injury (data not shown). Insecticide sprays had no effect on the incidence of these deformities except for an increase on 'Mic Mac' in 1990.

Discussion

The range of tarnished plant bug injury observed among the cultivars is consistent with previous research (Handley et al., 1991). The reduced injury observed for some cultivars may be explained by the relatively small number of tarnished plant bug nymphs found on these as compared to other cultivars. This observation suggests an oviposition preference by adults, a feeding preference by nymphs, or possibly an antibiosis mechanism within less susceptible cultivars which reduces nymph survival. If the differences in injury are based primarily on a feeding or an oviposition preference, the effect might be greatly diminished if only a nonpreferred host were available. Studies using large, isolated, single cultivar plots could determine if differences in susceptibility are dependent on the selection of cultivars available.

Tolerance to feeding may also reduce apparent injury. The tendency for cultivars with little apical seediness to have higher levels of other deformities may indicate that feeding damage is being expressed differently or that there is compensation for injury during fruit development. Alternatively, other deformities may have been overshadowed by the more severe apical seediness in susceptible cultivars and therefore were not counted. However, previous research has suggested that 'Honeoye' is less likely to exhibit apical seediness than other cultivars when exposed to tarnished plant bugs for equivalent amounts of time (Handley, 1991).

Avoidance is another possible reason for cultivar differences. Early flowering cultivars may escape injury by passing through the preferred oviposition or feeding stage before tarnished plant bugs are present in significant numbers. 'Honeoye', the cultivar least injured in this study, flowers relatively early, but other early flowering cultivars are known to be susceptible to injury (Handley et al., 1991), and some late flowering cultivars, such as 'Sparkle', show relatively little damage.

The results of this experiment suggest that insecticide applications could be reduced or eliminated in plantings of 'Honeoye' which include other cultivars known to be susceptible to tarnished plant bug injury. Insecticide applications may also be reduced in plantings of 'Honeoye' alone, providing that a low injury level can be sustained in large, single cultivar plantings. Although monocultures of this type have not yet been studied, the data show promise for the development of effective resistance through selective breeding programs. Relatively few strawberry genotypes have been screened for susceptibility to tarnished plant bug injury to date, but significant variation in injury levels has been observed. There are some indications that relative susceptibility to tarnished plant bug injury has a genetic basis (Handley et al. 1991). Further screening of strawberry germplasm for susceptibility to tarnished plant bug injury and investigations into the mechanisms of susceptibility are warranted.

Table 5.1. Numbers of tarnished plant bug nymphs recovered from sampling among six strawberry cultivars and three insecticide treatments in 1990 and 1991.

Cultivar	Number of insecticide sprays: None	One	Three
		1990 data	
Kent	8.18 abc[z]	9.38 ab	2.48 def
Honeoye	2.93 def	3.97 cde	0.78 f
Sparkle	5.45 abcd	4.83 bcde	1.72 def
Mic Mac	7.87 abc	7.66 abc	4.04 cde
Redchief	5.35 abcd	5.18 abcd	1.37 ef
Guardian	9.28 ab	10.64 a	4.63 bcde
		1991 data	
Kent	3.03 a	0.55 cde	0.13 de
Honeoye	1.21 abcd	2.68 a	0.00 e
Sparkle	1.75 abc	0.55 cde	0.13 de
Mic Mac	1.37 abc	1.48 abc	0.00 e
Redchief	1.04 bcde	1.56 abc	0.00 e
Guardian	2.24 ab	1.24 abcd	0.00 e

[z]Means adjusted by square root transformation. Means within a year followed by the same letter are not significantly different (Duncan's Multiple Range Test, $P = 0.05$).

Table 5.2. Marketable yield (grams/plot) of six strawberry cultivars with different numbers of malathion sprays.

Cultivar	Number of insecticide sprays		
	None	One	Three
		1990 data	
Kent	799 defgh[z]	1311 cde	3078 a
Honeoye	1346 cd	2345 b	2340 b
Sparkle	761 efgh	644 fghi	1473 c
Mic Mac	104 i	281 hi	1106 cdef
Redchief	339 hi	733 efgh	979 cdefg
Guardian	383 hi	458 ghi	868 defgh
		1991 data	
Kent	1592 cd	2737 b	3632 a
Honeoye	1890 c	2793 b	2839 b
Sparkle	970 de	1184 cde	1481 cd
Mic Mac	961 de	1445 cd	2713 b
Redchief	1266 cd	1450 cd	1910 c
Guardian	475 e	1043 de	1833 c

[z]Means within a year followed by the same letter are not significantly different (Duncan's Multiple Range Test, $P = 0.05$).

Table 5.3. Apical seediness (percent of yield in grams/plot) caused by tarnished plant bug among six cultivars and three levels of malathion sprays.

Cultivar	Number of insecticide sprays		
	None	One	Three
		1990 data	
Kent	46.0 bc[z]	35.6 cd	7.3 ghij
Honeoye	10.8 fghij	7.5 ghij	2.2 j
Sparkle	16.2 efgh	15.2 efgh	3.1 ij
Mic Mac	86.8 a	56.0 b	13.1 efghi
Redchief	36.4 cd	19.7 defg	5.6 hij
Guardian	29.6 cde	22.0 def	7.1 ghij
		1991 data	
Kent	33.7 a	11.7 bcdef	5.9 cdef
Honeoye	7.8 bcdef	5.5 def	1.4 f
Sparkle	16.4 bc	4.9 ef	1.1 f
Mic Mac	34.6 a	17.4 b	2.3 f
Redchief	18.4 b	14.5 bcde	1.2 f
Guardian	35.1 a	15.9 bcd	1.7 f

[z]Means within a year followed by the same letter are not significantly different (Duncan's Multiple Range Test, $P = 0.05$). 1990 means adjusted by arcsine transformation.

CHAPTER VI

SUMMARY

Strawberry malformation caused by the tarnished plant bug is a serious problem for farmers in northeastern North America. The experiments carried out in this study have demonstrated that "apical seediness," the injury most commonly associated with this insect, occurs as a result of feeding on blossoms from anthesis to shortly after petal fall. Under greenhouse conditions, the injury was most likely to occur after blossoms had been exposed to a single insect for 24 to 48 hours. While it is unclear what this might mean under field conditions, where numerous bugs may feed on a single blossom, it appears that apical seediness results when approximately 50% of the achenes in the apical area are affected, i.e., nonviable. Tarnished plant bug feeding at prebloom generally resulted in blossom death. This has not been reported under field conditions. Severity of injury decreased as feeding occurred later in flower development. Rather than apical seediness, various dents and creases were observed in receptacles from feeding following achene separation. Similar to blossom death, these deformities are not typically attributed to tarnished plant bug in the field, and therefore, these observations may be worthy of further study.

Light and scanning electron microscopy revealed that achenes are feeding sites for tarnished plant bugs on strawberry blossoms between anthesis and petal fall. This provides important evidence to support the hypothesis that apical seediness is caused by the destruction of the achenes following fertilization, which interrupts the synthesis of auxin in the endosperm and its translocation to the receptacle tissue. Cells in the receptacle fail to enlarge without an auxin stimulus from the achenes, resulting in the characteristic concentration of achenes or "buttoning."

Microscopy also revealed that tarnished plant bugs fed on receptacle tissue of more developed blossoms, once the achenes had become lignified, but this feeding was usually close to an achene. Sites close to achenes were probably sought because of the vasculature associated with achenes, which runs though the receptacle carrying nutrients. Based on the greenhouse studies, these feeding sites probably cause malformations such as indentations or creases in the receptacle. These malformations decreased in severity as feeding occurred later, because cell volume increased as berry development progressed, and therefore, fewer cells were affected.

Field experiments demonstrated significant variation in susceptibility to tarnished plant bug injury among 20 different strawberry cultivars. In small, randomized plots, 'Honeoye' had the least amount of fruit with apical seediness over two harvest seasons, significantly less than 12 other cultivars. 'Kent' and 'Mic Mac' had consistently high levels of injury. Some cultivars with low injury levels shared common parents, as did some cultivars with high injury levels, indicating that traits affecting susceptibility may be inherited.

When six cultivars, representing a range in susceptibility, were subjected to different insecticide treatments, 'Honeoye' again had injury levels lower than any other cultivar in the trial, and was not significantly affected by insecticide treatments. Thus, insecticide applications for tarnished plant bug could possibly be reduced or eliminated on some cultivars, such as 'Honeoye', at least when they are grown in the presence of other, susceptible cultivars, as was the case in this experiment. Whether reductions in insecticide applications are possible in large fields of single cultivars is not known, but may be doubtful given grower experience in this regard. However, these experiments have demonstrated significant variation in tarnished plant bug injury within a small genotype sample, indicating that the development of effective resistance to tarnished plant bug through selective breeding may be possible.

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